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# Spatial scales of variance in abundance of intertidal species: effects of region, dispersal mode, and trophic level

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*Abstract*. Determination of the pattern of variation in population abundance among spatial scales offers much insight into the potential regulating factors. Here we offer a method of quantifying spatial variance on a range of scales derived by sampling of irregularly spaced sites along complex coastlines. We use it to determine whether the nature of spatial variance depends on the trophic level or the mode of dispersal of the species involved and the role of the complexity of the underlying habitat. A least-cost distance model was used to determine distances by sea between all pairs of sites. Ordination of this distance matrix using multidimensional scaling allowed estimation of variance components with hierarchical ANOVA at nested spatial scales using spatial windows. By repeatedly moving these spatial windows and using a second set of spatial scales, average variance scale functions were derived for 50+ species in the UK rocky intertidal. Variance spectra for most species were well described by the inverse power law ($1/f^{\beta}$) for noise spectra, with values for the exponent ranging from 0 to 1.1. At higher trophic levels (herbivores and carnivores), those species with planktonic dispersal had significantly higher β values, indicating greater large- than small-scale variability, as did those on simpler coastlines (southwestern England and Wales vs. western Scotland). Average abundance and proportional incidence of species had the strongest influence on β values, with those of intermediate abundance and incidence having much greater large-scale variance ($\beta \approx 0.5$) than rare or ubiquitous species ($\beta \approx 0$).

*Key words: dispersal mode; habitat complexity; population connectivity; spatial scale; trophic level; variance.*

## Introduction

Analysis of spatial patterns contributes much to understanding processes structuring biological communities. Quantifying the relative magnitude of variance ($s^2$) at different scales, the variance spectrum, can be done with a variety of methods (Platt and Denman 1975, Horne and Schneider 1994, 1995). For irregularly spaced data the two most commonly used are 1) semi-variograms, based on variance between pairs of data separated by different distances, and 2) hierarchical analysis of variance with smaller spatial scales nested within larger ones. Each approach offers different advantages and disadvantages (Rossi et al. 1992, Hoef et al. 1993, Davidson and Csillag 2003). Pairwise use of data points for variograms removes artifacts introduced through arbitrary imposition of predefined spatial scales, but calculated variance includes variation up to and including the spatial scale of separation of points. Variograms also assume that mean values of the response are the same across the spatial domain. Hierarchical ANOVA independently quantifies variance on each spatial scale (Underwood and Chapman 1996), allowing significance testing. Tests against simulated data have shown that nested ANOVA does much better than semivariograms in detecting significant components of spatial variation (Davidson and Csillag 2003).

Power functions are often found to describe the pattern of variance with spatial scale very well. Variance spectra are commonly described by the inverse power law, where variance scales by $1/f^{\beta}$, where $f$ is the spatial frequency and $1/f$ is proportional to the spatial wavelength, also commonly fitted to temporal variation (Vasseur and Yodzis 2004). The exponent of this function, β, is a useful description of the spectrum, with values used to express environmental "noise color" (2, red; 1, pink; and 0, white). The value of β has proved more useful than measures of single characteristic scales of variation (Denny et al. 2004). The form of the variance spectrum, $s^2$ as a function of $f$, is distinct from that of spectral density ($s^2/f$): if $s^2$ is proportional to $1/f^{\beta}$, then $s^2/f$ is proportional to $1/f^{(\beta+1)}$.

Populations in fragmented habitats with barriers to spread or connected by complex corridors, such as rivers and streams, make application of variance scale methods difficult, since evaluating distance between sites must

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take account of these barriers to properly represent the spatial structure of the data. This applies particularly to sites on convoluted coastlines and islands. Simple geographical coordinates are not representative: sites on opposite sides of an isthmus may be geographically close (<10 km), but distant from each other by sea (>100 km). Such problems can be overcome using least-cost distance models (e.g., Adriaensen et al. 2003) to determine shortest routes between sites through biologically feasible connections; we use this approach in this paper.

Application of this method has allowed us to test hypotheses about the general form of variance spectra of abundance of species within their geographical ranges. Our first hypothesis was that variance spectra for species distributions reflect underlying variance in habitat quality or quantity over different spatial scales. Species from topographically more complex habitats should show greater variability on smaller scales than those from more uniform habitats, since habitat-related effects on abundance vary more on smaller scales in complex habitats than in homogeneous habitats. For intertidal habitats, straight, uniform coasts should have less small-scale variability than indented or fragmented coasts made up of shores of varying soft and hard substrata. Around the United Kingdom, the fjordic landscape of west Scotland is more complex than the largely straight coastline of southwest England. We aimed to exploit this difference to assess the "complexity" hypothesis by measuring complexity for each region and contrasting the form of variance spectra for species between the regions.

Influences on variance spectra for organism abundance have been most fully explored in the oceanographic literature (Platt and Denman 1975, Denman and Platt 1976). For planktonic species, essentially passive tracers of turbulent water motion, a $-5/3$ scaling is expected, reflecting the Kolmogorov cascade of potential energy from large to small scales. Phytoplankton species generally tend to follow this prediction, but higher-trophic-level consumers, such as krill in the Southern Ocean (Weber et al. 1986), tend to have flatter spectra. One mechanism suggested for this difference is that aggregation of predators "injects" variance at small scales, leading to lower $\beta$ values for their spectra.

Intertidal organisms are also influenced by these oceanographic processes, yet are generally far less mobile than planktonic species, and their spatial distributions are not directly shaped by the turbulent dissipation of kinetic energy. Instead, lower-trophic-level species tend to be controlled by spatially autocorrelated bottom-up processes (nutrients, light, and temperature), leading to primary producers such as macroalgae having increasing variance at larger scales (Broitman and Kinlan 2006). Higher-trophic-level species in the intertidal, on the other hand, tend to be mobile, preferentially associated with particular microhabitats acting as refuges or with patches of prey (Underwood and Chapman 1996), and may respond numerically to high food supply on small scales over short timescales (Fischer-Piette 1935, Hughes and Burrows 1993), all processes injecting variance on small scales. Comparing variance spectra for rocky-shore species at different trophic levels allowed us to test the generality of the hypothesis that higher-trophic-level species have flatter variance spectra.

The mode of reproductive dispersal of an organism also affects its variability over different spatial scales. Short-distance dispersal can result in greater small-scale variability (Johnson et al. 2001) than long-range dispersal. The latter may reduce small-scale variability by synchronizing population fluctuations in neighboring sites (Burrows et al. 2002), by stabilizing interactions between strongly interacting species (Hassell et al. 1994), and by regularly reestablishing populations in small areas where stochastic processes may otherwise lead to extinction. By comparing variance spectra of short-distance dispersers with spectra of long-distance dispersers, we tested our third hypothesis: that long-distance dispersal leads to less variability on smaller spatial scales.

The final pattern may depend upon the balance between intrinsic (such as behaviour and population dynamics) and extrinsic (responses to environment and other species) influences on scales of spatial variance (Levin 1992). In coastal systems, for example, there is a growing recognition of the importance of nearshore oceanographic conditions for the dynamics of communities, especially for those elements of the community directly reliant on planktonic food, such as barnacles (Sanford et al. 1994, Sanford and Menge 2001, Leslie et al. 2005). Similarity of scales of spatial variation in distributions with those of their putative causes can give important corroborative evidence for the hypothesized links between patterns and processes.

In this study we aimed to quantify spatial variance at a range of spatial scales from 10 to 1000 km for abundance of over 50 rocky shore species in two separate regions of the UK coast. By ordination of inter-site distance matrices into 2-D space using multidimensional scaling (MDS) and subsequently repeatedly applying hierarchically nested ANOVA using sets of overlapping spatial scales and moving spatial windows, we obtained smooth functions for variance as a function of spatial scale. Using independently derived variance spectra from the two UK coastal regions, we planned to test hypotheses on the effects of species' trophic level and dispersal mode on variance spectra and contrast differences in spectra from areas of different coastal complexity.

## Materials and Methods

### *Rocky shore surveys*

Most of the UK rocky intertidal coastline was surveyed at ~30-km intervals in July and August of 2002, 2003 and 2004, with each site visited once only (see Plate 1). In our choice of sites at the 10–30 km scale we

aimed to visit locations over the full range of physical conditions in the area, from wave shelter to wave exposure. Site choice was also guided by accessibility. We aimed at four site visits over a 4-h period spanning low tide and achieved this by selecting shores in close proximity to roads with no more than 40-min travel time between each site.

The emphasis of this study was to obtain rapid abundance estimates for the maximum number of species. Every species on a predefined checklist was assigned to a single abundance category based on quadrat counts or visual assessment of the percent cover in the area of that species' greatest abundance on the shore. The process took ~1 h to record all the species on the checklist and covered the entire intertidal area over 50–200 m of shoreline. If the species was not seen during the shore survey despite a search, it was recorded as not found. Six abundance categories were used as defined by Crisp and Southward (1958) and modified by Hiscock (1981) with approximately two categories spanning each order of magnitude. Full details of the application of the assessment procedure and categorical scales for each species are given in Burrows et al. (2008), as well as a validation of the method against estimates of abundance from quadrat-based measures for selected species. Each survey was done within 2 h of the time of low water predicted for that date and location. The location was recorded at mid-shore using a handheld geographic positioning system (GPS; Garmin GPS72, accurate to <15 m for 95% of operation; Garmin, Southampton, UK). Two subsets of this data set were used to assess the effects of broader region on spatial variance spectra: 225 sites from the English Channel (50°45′38″ N, 0°6′46″ E) to North Wales (53°18′41″ N, 3°44′17″ W) and 186 sites on Scottish coasts on the mainland and nearby islands from Ayrshire (55°3′36″ N, 5°4′12″ W) to Orkney (59°16′32″ N, 2°23′57″ W). For the purposes of this analysis, differences among sites were assumed to be due to spatial location and not to temporal variation, despite the three-year duration of the survey. Resurveys of 26 sites in Scotland in 2006 gave a high correlation between new and prior abundance scores (Kendall's $\tau_b = 0.375$, $n = 1224$ scores, $P < 0.001$), suggesting that the spatial patterns were sufficiently persistent to justify this assumption. Some caution should nonetheless be applied in interpreting spatial variance patterns when these are produced from surveys done at different times.

### *Wave fetch, coastline complexity, and remotely sensed temperature and chlorophyll*

To compare variance spectra of species abundance with those of underlying environmental variables, site-specific values of wave fetch, seasonal sea surface temperature (SST), and chlorophyll *a* (chl *a*) were extracted from larger data sets. Wave fetch was determined for all 200-m coastal cells in the two study areas using an iterative method to find the nearest land in 22.5° angular sectors, up to a maximum distance of 200 km (Burrows et al. 2008). Site values were taken from nearest coastal grid cells. Coastline complexity was determined for the two regions using the box-counting method (Appendix A). We acknowledge that the comparison between levels of coastline complexity is spatially confounded since we have only one region for each level. However, our main purpose here is to illustrate the application of the procedure rather than testing a causal hypothesis about the effect of coastal complexity on variance spectra. The SSTs were obtained from monthly satellite image composites (AVHRR Pathfinder data 0.044° 4.5-km grid, *available online*),[6] averaged separately for the months of February, May, August, and November over the period 2000–2006. Chlorophyll *a* data were obtained for the same period (SeaWIFS 0.018° 2-km grid; European Commission, Ocean Colour Portal, *available online*).[7] Both sets of remotely sensed data had a 5–15 km coastal mask. Neighborhood averaging of pixel values over this radius allowed assignment of SST and chl *a* to coastal survey sites. Values for sites far from the coast were taken from the nearest open-water pixels.

### *Distance estimation*

Good estimates of the effective separation distance are needed to quantify the variability between samples as a function of their spatial separation. In this study we took the most representative measure of separation to be the shortest sea route between sites, calculated using a cost-distance method applied repeatedly using each sample site as the center (Appendix A). This sampling space was recast to better reflect the separation distance of sites by processing the site-to-site distance matrix using multidimensional scaling (PROC MDS; SAS Institute 2004) to position sites in a 2-D space such that far-separated sites from the distance matrix were far apart and nearby sites were close to one another (Appendix A: Fig. A2).

### *Scale variance in species abundance and environmental conditions*

Variance was separately calculated for two sets of nested spatial scales (400, 200, 100, 50, and 25 km and 300, 150, 75, 37, and 20 km), giving 10 distance classes. Preliminary analyses using example species showed that more distance classes gave smoother variance spectra, but that the additional classes had little effect on the estimated spectral exponent (β). Each site was assigned to square regions based on MDS coordinates for each step in one of the spatial scales (Appendix A: Fig. A2). Species abundance categories were replaced with integer values (0, not found; 1, rare; 2, occasional; 3, frequent; 4, common; and 5, abundant) before entering a fully nested random effects ANOVA (PROC GLM; SAS Institute 2004) with scale effects entered in order from largest to

[6] ⟨http://poet.jpl.nasa.gov/⟩
[7] ⟨http://marine.jrc.cec.eu.int/⟩

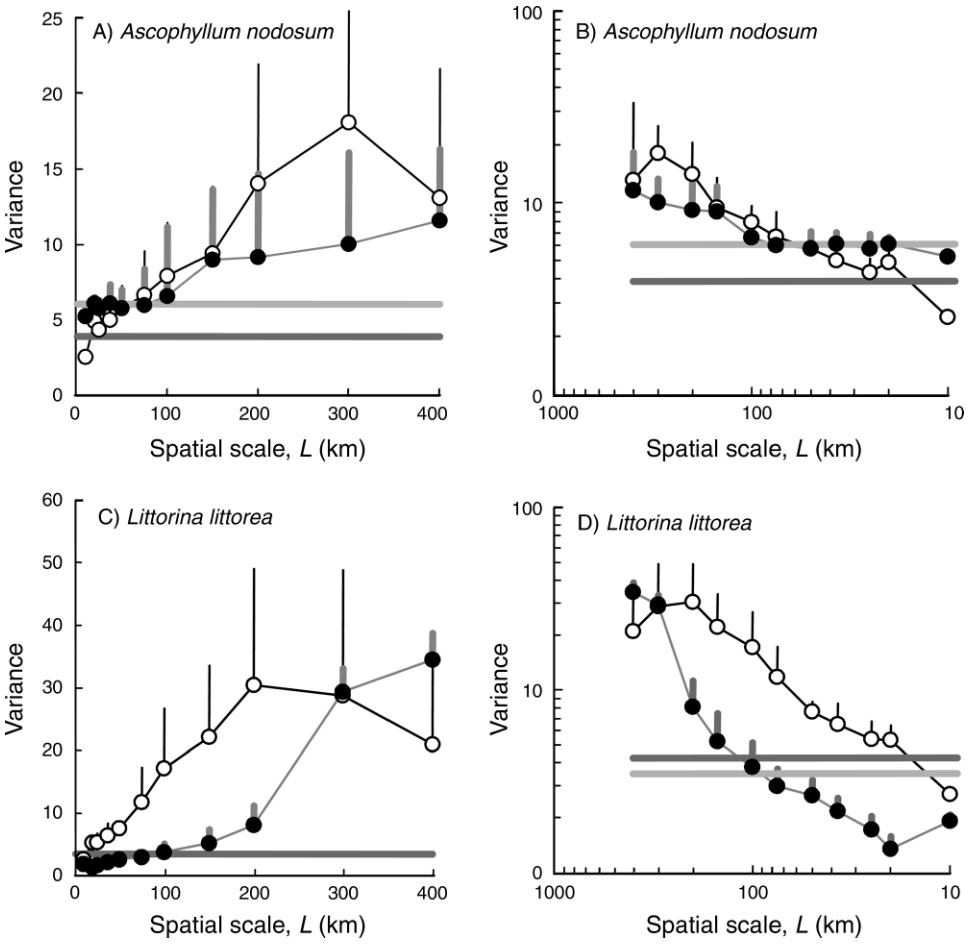


FIG. 1. Spatial scale variance spectra for two example species: (A) the macroalga *Ascophyllum nodosum* and (C) the grazing snail *Littorina littorea* (bottom) in southwestern England and Wales (open symbols) and western Scotland (solid symbols). Scale variance values are shown as means + SD. Panels B and D show the same variance spectra on log scales. Horizontal bars show among-site variance for each region (light gray, western Scotland; dark gray, southwestern England and Wales).

smallest. Variance estimates for each spatial scale were derived from Type I sums of squares and degrees of freedom. The process was repeated 12 times for each set of nested scales by shifting the origin of the coordinate system by a fixed amount each time (37 km for scale 1 and 40 km for scale 2) to average out the effect of an arbitrary point of origin. Means and standard deviations of variance estimates were calculated for each spatial scale. The nested ANOVA approach is similar but not the same as spectral techniques more commonly used elsewhere, such as spectral analysis (e.g., Denny et al. 2004), which are generally not applicable to irregularly spaced data.

The analysis was done for abundance of 71 species in the Scottish data set and 51 species in the English and Welsh data set. Twenty-nine species were analyzed in both regions. Some species that are found in England and Wales were absent from Scotland (Southward et al. 1995), while others recorded in the northern region were not recorded in the southern region. The method was also applied to site-specific values of wave fetch, monthly average SSTs (February, May, August, November), and chl *a*.

Patterns of variance (Fig. 1) showed general increasing trends with spatial scale ($L$, where $L = 1/f$) that could be described by power functions. The data follow the expectation of $1/f$ noise with spatial scale. Exponents ($\beta$ values) of power functions were calculated for each species in each region by linear regression of the log-transformed variance on log(distance), $L$ (Denny et al. 2004). Significance of $\beta$ values was assessed with $t$ tests of the difference of each $\beta$ value from zero (Zar 1984).

To assess the validity of our method, we generated 2-D field data with known values of $\beta$ and compared the estimates of the spectral exponent obtained with the ANOVA approach to the nominal values used in the simulations (Appendix B).

### *Comparisons among regions, trophic levels, modes of dispersal, and with species incidence*

The data set of estimates was used to compare the patterns of spatial variation among species in different

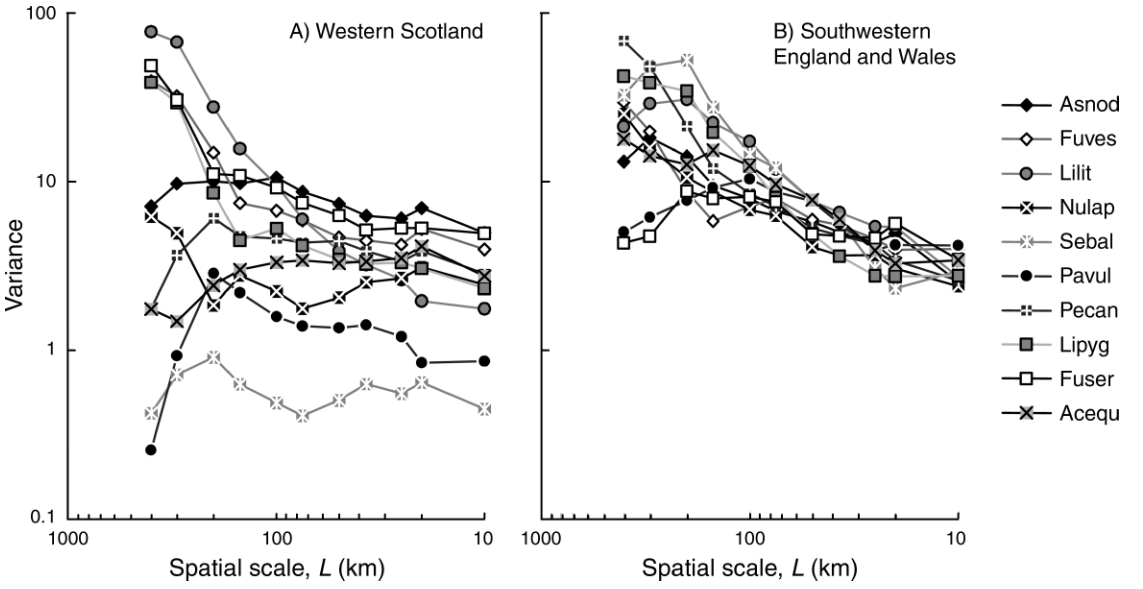


FIG. 2. Variance spectra for the 10 most abundant species at (A) western Scotland sites and (B) southwestern England and Wales. Species abbreviations are shown in Table 3.

regions, among trophic levels, and among rare and abundant species. Species were assigned to one of three trophic levels (0, primary producers; 1, herbivores, including filter feeders and grazers; and 2, carnivores). The mode and estimated duration of dispersal were determined for each species from published studies (Appendix C). Species were classed either as non-planktonic dispersers, producing egg capsules or live young, or as planktonic dispersers, producing planktonic propagules, including macroalgal zoospores and planktonic larvae. Preliminary analysis showed no significant regression of β on dispersal duration for planktonic dispersers, so further analyses were based on comparison of the two dispersal categories.

An unexpected emerging finding was the strong effect of the proportional incidence of each species on variance spectra. Incidence was determined for the data sets in each region, defined as the proportion of sites at which the species was recorded as present (at least rare). Effects of region, trophic level, dispersal mode, and incidence of species in regional data sets were analyzed by least-squares model fitting and model selection based on information theoretic methods (Johnson and Omland 2004). Region, trophic level, and dispersal mode were all considered as fixed effects. Akaike's Information Criterion corrected for small sample sizes ($AIC_c$) was calculated for a range of regression models including all combinations of the three factors, region, trophic level, and dispersal mode as main effects plus their two-way interactions. The $AIC_c$ is based on the goodness of fit of the model (residual sums of squares) and the number of fitted parameters, such that an increase in fit due to inclusion of more parameters is penalized in such a way as to reveal the most parsimonious model from a range selected. A second set of models was evaluated that included these terms in combination with a quadratic function of proportional incidence. The smallest $AIC_c$ value was used to select the best model from each of the two sets with and without the proportional incidence of each species.

## RESULTS

### *Scale variance*

Variance increased with spatial scale for the majority of species (regression slopes $P < 0.05$ for 53 out of 71 [75%] species in western Scotland and 39 out of 52 [75%] in southwestern England and Wales). Variability in estimates of variance also increased with spatial scale (see error bars on Fig. 1). Changing the extent of spatial windows thus had a much greater effect on the estimate of spatial variance at larger scales than smaller scales.

The sequential ANOVA technique with moving spatial windows successfully returned values close to the spectral exponent of the 2-D simulated data for large samples. A large sample size ($n = 1000$) gave estimates of β centered on the value used to simulate the distribution (Appendix A: Fig. A2A), while smaller sample sizes underestimated β (by 0.7–1.0 for $n = 50$ and by 0.5 for $n = 200$; Appendix A, Fig. A2A, B).

Changes in variance shown in Fig. 1 were typical of most species examined. In western Scotland most species showed an increase in scale variance from the 10-km scale up to the 200-km scale (Fig. 2A). At larger scales (>200 km) the pattern in variance was much more variable among species. Some species showed a sharp decline (*Semibalanus balanoides*, *Pelvetia canaliculata*, *Patella vulgata*) in variance at the largest scales (200–400 km) compared to smaller scales (<200 km), while others

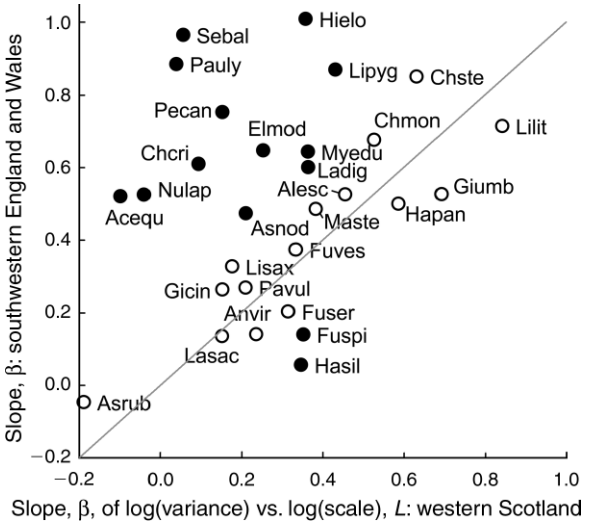


FIG. 3. Slopes of regressions of log(variance) vs. log(scale) (β values) for species present both in western Scotland and southwestern England and Wales. Line indicates equality. Solid symbols show significant differences ($t$ test, $P < 0.05$). Species abbreviations not listed in Table 3 are given in Appendix C.

showed a considerable increase in variance at larger scales (*Littorina littorea*, *Fucus serratus*, *Lichina pygmaea*). A similar range of patterns was seen for the same species in southwestern England and Wales (Fig. 2B): steady increase in variance up to 200 km and greater diversity of patterns at larger scales.

Twenty-nine species were recorded in both regions, and 12 of these had significantly different β values between the regions ($P < 0.05$ for $t$ tests for difference between estimates, df = 11, see Fig. 3). There was a significant positive correlation between β values in the two regions ($r = 0.342$, one-tailed $P = 0.034$), but very large differences for some species, notably *Semibalanus balanoides* and *Pelvetia canaliculata*, with large β values in the southwest and small β values in Scotland and *Littorina littorea* showing the opposite pattern. Proportional incidence among these 29 species was strongly correlated between the two regions ($r = 0.610$, one-tailed $P = 0.0002$): rare species tended to be rare and common species common in both areas.

Variance spectra of environmental variables had higher β values than those for species abundance (Fig. 4, Table 1). With the exception of summer SSTs, β values for spectra in southwestern England and Wales were higher than those in western Scotland. The reversal of the tendency for higher environmental β values on a less complex (and higher β) coastline for summer temperatures was associated with some small-scale upwelling features (e.g., St Ives Bay) in a generally stratified coastal ocean off southwestern England. Western Scotland summer sea temperatures, in contrast, were characterized by a single large stratified area, the Clyde Sea, in the midst of an otherwise tidally well-mixed sea, leading to dominance of the spectrum by large-scale variance. Variance spectra for wave fetch had much lower β values (~0.4) than those for SST and chl *a* (1.3–2.1).

### *Comparisons among regions, trophic levels, modes of dispersal, and with species incidence*

For models without proportional incidence as a predictor, the model with the lowest $AIC_c$ value was a

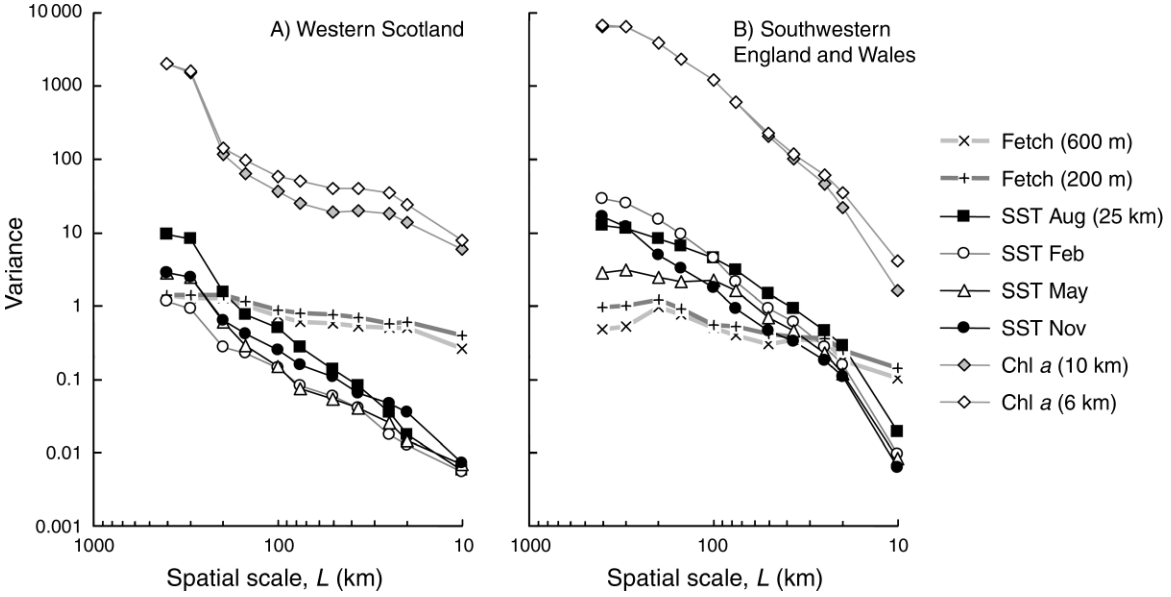


FIG. 4. Variance spectra for seasonal sea surface temperatures (SST, °C), mean chlorophyll *a* (chl *a*, using original pixel values), and wave fetch at (A) western Scotland sites and (B) southwestern England and Wales. Distances in the symbol key indicate the radius of local averaging used to derive site-specific values.

TABLE 1. Exponents (β) of power functions fitted to variance spectra for site-specific values of estimated total wave fetch; spatially averaged, remotely sensed sea temperatures; and chlorophyll *a* values and β values for coastline complexity for the two study regions: southwestern England and Wales and western Scotland.

| Environmental variable | β | |
|---|---|---|
| | Western Scotland | Southwestern England and Wales |
| Wave fetch | 0.42 | 0.45 |
| Sea surface temperature 2000–2006 | | |
| February | 1.44 | 2.07 |
| May | 1.66 | 1.41 |
| August | 2.01 | 1.59 |
| November | 1.51 | 1.92 |
| Chlorophyll *a* | 1.30 | 2.01 |
| Coastline complexity | 1.54 | 1.76 |

PLATE 1. The rocky intertidal of a moderately wave-exposed shore at Cullercoats in northeast England, showing a typical mid- to low-shore mosaic of macroalgae, barnacles, and bare rock. A 0.5-m quadrat is shown in the foreground. Photo credit: M. T. Burrows.

main effects model with trophic level and region terms (Table 2). Removal of either of these terms had a highly significant effect on the model fit, while addition of dispersal mode had no significant effect (Table 2). Species in the southwest of England and Wales tended to have larger β values (southwestern England and Wales relative to western Scotland, $0.209 \pm 0.050$ [coefficient ± SE], $P < 0.001$). Predators tended to have smaller β values than primary producers and consumers (relative to primary producers; primary consumers, $+0.047 \pm 0.053$, $P > 0.05$; predators, $-0.270 \pm 0.078$, $P < 0.001$). The main effects model reproduced the pattern among the observed means relatively well (Fig. 5).

The most striking effect was that of proportional incidence (Fig. 6). Rare and ubiquitous species tended to have low or near-zero β values, while those only present in about half of the sample sites in each region tended to have the largest β values. The quadratic function captured this trend well. The lowest $AIC_c$ of the models that included incidence was for that including all three main effects terms (trophic level, region, and dispersal mode) and the interaction term of trophic level and dispersal mode (Table 2). Removing the interaction from this model gave significant increases in residual sums of squares. Thus, after accounting for the effect of proportional incidence, the difference between regions

TABLE 2. Selection of regression models for variance (β) values.

| Term dropped | Model | *k* | $AIC_c$ | *R* df | RSS | Change in df | Change in RSS | *F* | Pr(>*F*) | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Models without proportional incidence (*I*) | | | | | | | | | | |
| | $T + R + D$ | 6 | 16.71 | 103 | 6.61 | | | | | 0.26 |
| Region (*R*) | $T + D$ | 5 | 32.33 | 104 | 7.78 | 1 | 1.170 | 18.24 | <0.001 | |
| Trophic level (*T*) | $R + D$ | 5 | 21.89 | 105 | 7.19 | 2 | 0.586 | 4.57 | 0.013 | |
| Dispersal mode (*D*) | $T + R$ | 4 | 15.48 | 104 | 6.65 | 1 | 0.047 | 0.73 | 0.395 | 0.26 |
| Region (*R*) | $T$ | 4 | 30.46 | 101 | 6.58 | 1 | 1.133 | 17.72 | <0.001 | |
| Trophic level (*T*) | $R$ | 3 | 26.76 | 106 | 7.66 | 2 | 1.011 | 7.90 | 0.001 | |
| Models with proportional incidence (*I*) | | | | | | | | | | |
| | $I + I^2 + T + R + D + T{:}D$ | 10 | −27.04 | 99 | 4.09 | | | | | 0.54 |
| T:D interaction | $I + I^2 + T + R + D$ | 5 | −24.08 | 101 | 4.36 | 2 | 0.272 | 3.29 | 0.041 | |

*Notes:* Model "$T + D$" omits the Region term from the model, for example, and the change in residual sums of squares from the full model "$T + D + R$" to the "$T + D$" model gives the test for significance (*F* ratio and *P*) for the Region effect. Abbreviations are: *k*, number of parameters; *R* df, RSS, residual degrees of freedom and sums of squares, respectively; df, numerator degrees of freedom.

remained (southwestern England and Wales, 0.186 ± 0.042, $P < 0.001$). However, the significant differences among trophic levels became dependent on modes of dispersal (Fig. 5B), suggesting that differences in the mean incidence of predators (mean $I = 0.26$) from consumers ($I = 0.39$) and primary producers ($I = 0.34$) may have been sufficient to account for the original differences in β values. As rarer species, predators would thus be expected to have lower β values.

Differences in proportional incidence between the two regions, for those species recorded in both, may also partly explain differences in β values. Differences predicted from the regression model (Fig. 6) were significantly positively correlated with observed differences in β values between Scotland and the southwest ($r = 0.379$, one-tailed $P = 0.025$). Thus the higher β values of the barnacle *Semibalanus balanoides*, for example, in the southwest compared to that in Scotland is associated with a change from almost complete ubiquity in Scotland ($I = 0.99$) to lower incidence in the southwest ($I = 0.69$, Table 3). Likewise the macro-alga *Halidrys siliquosa* was rarer in the southwest than in Scotland, but because the change was from $I = 0.29$ in Scotland to 0.15 in the southwest, this was associated with a decrease in β (Fig. 3).

Mean abundance and variance in abundance were both closely related to proportional incidence and therefore were also related to β values. Mean abundance was almost exactly proportional to incidence ($r = 0.98$), while variance followed a dome-shaped function of abundance and proportional incidence well fitted by quadratic regressions ($R^2 = 0.89$ and 0.85, respectively). The β values were thus linearly related to variance and had a similar relationship with abundance to that of incidence.

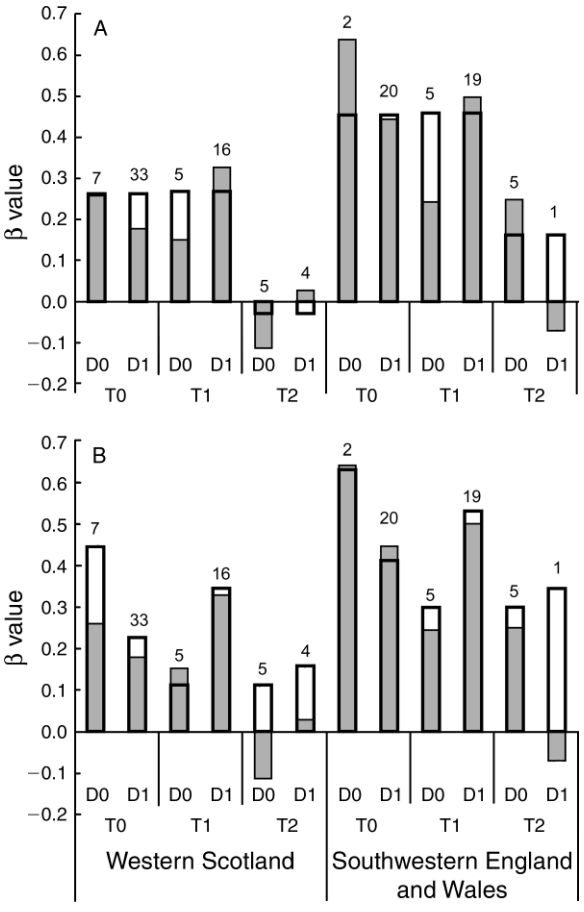


FIG. 5. Variance scale slopes (β values) among regions, trophic levels, and modes of dispersal. Gray bars show means, bold outlined open bars show fits for the model (A) without species incidence and (B) with species incidence (where $I = 0.5$). Numbers above bars indicate the number of species in each group. Trophic levels: 0, primary producers; 1, herbivores; 2, carnivores. Dispersal modes: 0, non-planktonic; 1, planktonic.

## DISCUSSION

We believe that this approach offers a robust and easily applied method for quantifying spatial variance in abundance over an almost continuous range of spatial scales in both marine and terrestrial systems, from relatively sparse and irregularly spaced data. Problems of complex connections can be solved by using relatively simple least-cost distance models to determine the shortest distance between sites. In our study of marine coastlines the principal barrier to species connections was the land mass, but for other systems the connections could be along habitat corridors (such as rivers and streams) or be barred by inhospitable habitats such as mountain ranges and deserts, or even towns, cities, and highways. Once the distances between all the sites in the study have been more realistically rendered in 2-D space using techniques such as multidimensional scaling or similar, it is a straightforward task to calculate variance estimates using hierarchical or nested analyses of variance based on windows of varying spatial scale. By shifting the spatial frame of reference of these windows and applying more than one set of nested spatial scales, it is possible to produce useful synoptic views of the patterns of spatial variability in population abundance of a large number of species. This has given us a rich set of data for testing hypotheses about causes of differences in spatial patterns among species in different geographical regions, with different levels of abundance, different trophic levels, and different dispersal patterns.

### *Variance scales and species incidence*

The largest influence on the slope of the variance spectra was the rate of occupancy of sites (incidence) of the species involved. The slopes of the variance spectra were strongly positively related to the total variance for each species ($r = 0.58$). Several reasons suggest themselves. Species abundance is bounded at species absence and at its usual upper limit, an effect completed by the categorical scale used here, making abundance effectively binomial over a wide-enough range of values. A hump-shaped relationship between variance and mean is

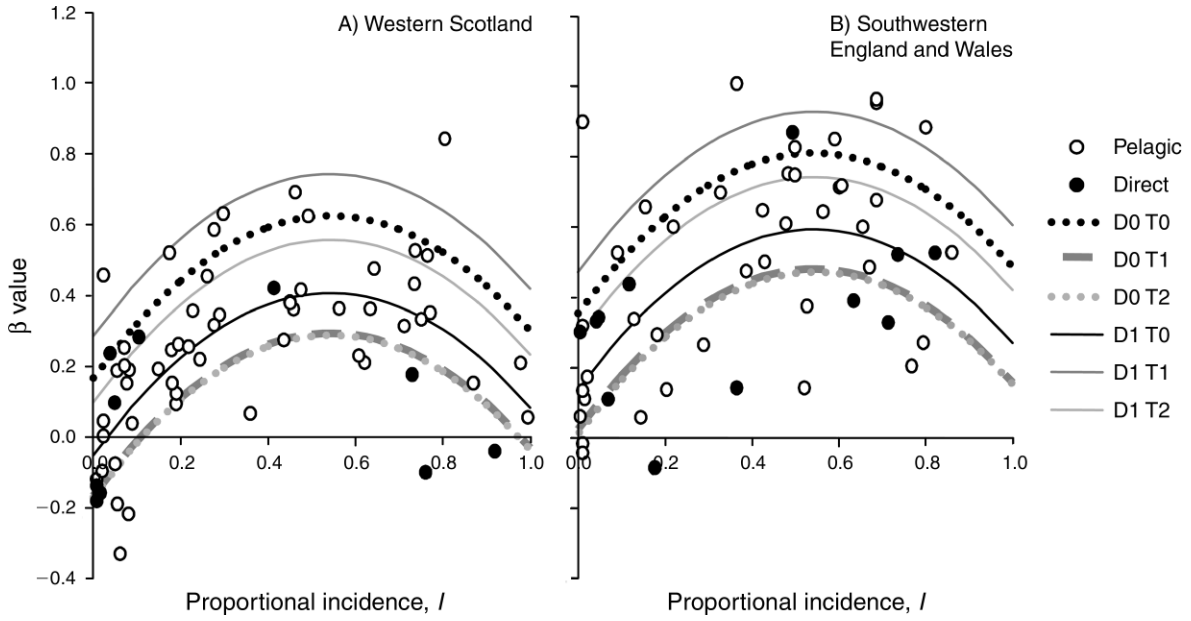


FIG. 6. The effect of proportional incidence of species on the slope of their spatial variance spectra, β, (A) for 71 species in western Scotland and (B) for 52 species in southwestern England and Wales. Open symbols show predicted values for non-planktonic dispersers (D1 in the key), and solid symbols are for planktonic dispersers (D0). Different fitted lines are shown for each dispersal mode (D0, D1) and trophic level (T0, primary producers; T1, herbivores; T2, carnivores) combination.

expected for binomial variables (average = $np$; variance $\sigma^2 = np(1 - p)$ where $n$ is the number of trials and $p$ is the probability of success). When variance is reduced at extreme low and high levels of average abundance, the method is less able to decompose variance into different nested scales. In addition, species present at around half of the survey sites ($I = 0.5$) are more likely to be straddling major biogeographical boundaries or nearing their range edges (e.g., *Semibalanus balanoides* and *Pelvetia canaliculata* in southwestern England; Crisp and Southward 1958, Southward et al. 1995) and thus likely to show more variability at larger scales and hence high β values.

### *Variance scales and trophic levels*

Reasons why predators should show greater small-scale variability than lower trophic levels, and thence lower β values, are not immediately obvious. For predatory whelks on rocky shores, Denny et al. (2004) found that *Nucella lamellosa* had the lowest β value of the species considered, while Underwood and Chapman (1996) also found that *Morula marginalba* had greater variance at smaller (0.1–10 m) than at larger (100 m–30 km) spatial scales. These studies considered trends in variance in abundance over smaller spatial scales (0.1 m–30 km, 0.1–500 m), thereby involving different sets of processes (Wiens 1989) to those in the present study (10–1000 km). A similar effect of trophic level occurs in other systems. Fasham (1978) found that increasingly larger size classes of plankton had progressively flatter variance spectra in plankton samples taken over a 200-km transect sampled at ~1 km intervals. Similarly, krill have been found to have flatter variance spectra than their phytoplankton food (Weber et al. 1986), attributed to aggregative behavior, also evident in intertidal snails (Feare 1971). However, our survey-based estimates averaged abundance over scales larger (100 m+) than snail aggregations (<1 m), so it seems unlikely that aggregation would have been the cause of the patterns seen for *Nucella lapillus*.

The reduced abundance of predators relative to other trophic levels may be the ultimate cause of their flatter variance spectra. Other rare species in this study had similarly low β values, and once the effect of differences in incidence were accounted for, the difference between trophic levels disappeared.

Spatial models of predator and prey populations offer no consistent expectations of the relative variance spectra of predators and prey, except the general expectation that the two should be linked. Mobile, higher trophic levels may encounter less mobile or sessile prey populations over a wider spatial scale (Holt 1996) and thereby may be expected to have less, not more, small-scale variability in population abundance. On the other hand, species–area relationships have been predicted to be stronger at higher trophic levels (Holt et al. 1999) because higher levels may depend on the presence of their food species and may not be present even in the presence of their food. Considered in the context of spatial scales, this implies that predators may be more likely to go extinct in small areas through stochastic small-population effects, resulting in more variability on smaller spatial scales. This explanation fits well with the general observation of a trend of decreasing β values

TABLE 3. Exponents (β) of power functions fitted to variance spectra and proportional incidence among sites ($I$) for 32 of the rocky-shore species used in this study, divided into five functional groups.

| Species | Abbreviation | $T$ | $D$ | Western Scotland β | Western Scotland $I$ | Southwestern England and Wales β | Southwestern England and Wales $I$ |
|---|---|---|---|---|---|---|---|
| Predators | | | | | | | |
| *Nucella lapillus* | Nulap | 2 | 0 | −0.04† | 0.92 | 0.53*** | 0.82 |
| *Actinia equina* | Acequ | 2 | 0 | −0.10† | 0.76 | 0.52*** | 0.74 |
| *Lipophrys pholis* | Lipho | 2 | 1 | 0.19*** | 0.15 | | |
| *Carcinus maenas* | Camae | 2 | 1 | 0.20** | 0.07 | | |
| Grazers | | | | | | | |
| *Patella vulgata* | Pavul | 1 | 1 | 0.21* | 0.98 | 0.27** | 0.80 |
| *Littorina littorea* | Lilit | 1 | 1 | 0.84*** | 0.81 | 0.71*** | 0.60 |
| *Littorina saxatilis* agg. | Lisax | 1 | 0 | 0.18*** | 0.73 | 0.33** | 0.72 |
| *Gibbula umbilicalis* | Giumb | 1 | 1 | 0.69*** | 0.46 | 0.53*** | 0.86 |
| *Littorina obtusata* | Liobt | 1 | 0 | 0.42*** | 0.41 | | |
| Filter feeders | | | | | | | |
| *Semibalanus balanoides* | Sebal | 1 | 1 | 0.06† | 0.99 | 0.97*** | 0.69 |
| *Chthamalus montagui* | Chmon | 1 | 1 | 0.53*** | 0.74 | 0.68*** | 0.69 |
| *Mytilus edulis* | Myedu | 1 | 1 | 0.36*** | 0.63 | 0.64*** | 0.56 |
| *Chthamalus stellatus* | Chste | 1 | 1 | 0.63*** | 0.30 | 0.85*** | 0.59 |
| *Halichondria panicea* | Hapan | 1 | 1 | 0.59*** | 0.28 | 0.50*** | 0.43 |
| Lichens | | | | | | | |
| *Verrucaria maura* | Vemau | 0 | 1 | 0.51*** | 0.77 | | |
| *Verrucaria mucosa* | Vemuc | 0 | 1 | 0.42*** | 0.48 | | |
| *Xanthoria parietina* | Xapar | 0 | 1 | 0.38*** | 0.45 | | |
| *Lichina pygmaea* | Lipyg | 0 | ... | 0.43*** | 0.44 | 0.87*** | 0.49 |
| Macro-algae: perennials | | | | | | | |
| *Pelvetia canaliculata* | Pecan | 0 | 1 | 0.15** | 0.87 | 0.75*** | 0.48 |
| *Fucus spiralis* | Fuspi | 0 | 1 | 0.35*** | 0.77 | 0.14* | 0.52 |
| *Fucus vesiculosus* | Fuves | 0 | 1 | 0.33** | 0.75 | 0.37*** | 0.53 |
| *Fucus serratus* | Fuser | 0 | 1 | 0.31** | 0.71 | 0.20* | 0.77 |
| Lithothamniacea, high-level pools | Lihig | 0 | 1 | 0.48*** | 0.64 | | |
| *Ascophyllum nodosum* | Asnod | 0 | 1 | 0.21*** | 0.62 | 0.47*** | 0.39 |
| *Laminaria digitata* | Ladig | 0 | 1 | 0.36*** | 0.56 | 0.60*** | 0.66 |
| Lithothamniacea, low shore rock | Lilow | 0 | 1 | 0.62*** | 0.49 | | |
| *Corallina officinalis* | Cooff | 0 | 1 | 0.36*** | 0.46 | | |
| *Cladophora rupestris* | Clrup | 0 | 1 | 0.23*** | 0.61 | | |
| Macro-algae: ephemerals | | | | | | | |
| *Enteromorpha* spp. | Enter | 0 | 1 | 0.43*** | 0.74 | | |
| *Scytosiphon lomentaria* | Sclom | 0 | ... | 0.34*** | 0.34 | | |
| *Ceramium* spp. | Ceind | 0 | 1 | 0.22* | 0.24 | | |
| *Porphyra umbilicalis* | Poumb | 0 | ... | 0.41*** | 0.24 | | |

*Notes:* Abbreviations are: $T$, trophic level (0, primary producers; 1, herbivores; 2, carnivores); $D$, dispersal mode (0, non-planktonic; 1, planktonic; ..., not determined). Significance of β values: † $P > 0.05$; * $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $0.001 > P$.

with increasing rarity. The link between scales of spatial variance and species–area relationships needs further theoretical development.

### *Variance scales, scales of dispersal, and population connectivity*

Scales of variation in population abundance should be strongly linked to the spatial scale of dispersal. Species with short-range dispersal (<1 km) may show more variability on smaller spatial scales, since recruitment will be linked to adult population densities over a small region: the spatial scale of a "closed" population. Conversely, species with long-range dispersal (>20 km) may have propagule supply and recruitment determined by average population densities over larger spatial scales. This spatial scale is usually so large that marine species with widespread larval dispersal are often considered as having "open" populations (Roughgarden et al. 1985). Ultimately though, even open populations can be considered as closed at sufficiently large spatial scales (Hughes et al. 2000). Our results showed that non-planktonic dispersal was linked to flatter variance spectra than species with long-duration/distance dispersal. Differences in scales of spatial variance between long- and short-distance dispersers has been seen before for intertidal gastropods (Johnson et al. 2001), with species lacking a planktonic dispersal phase showing more variability at smaller (<100 m) than at larger (5–20 km) spatial scales. Increased dispersal can allow persistence of unstable interactions, as spatial versions of models of such interactions show (e.g., Hassell et al. 1991). Species with limited dispersal may well therefore

be more likely to "boom or bust" at local scales, beyond the simple stochastic effects of small population sizes.

The observed link between dispersal scales and β values goes some way towards validating the use of scales of dispersal in designing targeted marine protected areas (Palumbi 2003, Shanks et al. 2003), with small reserves for short-dispersed species. Such species emerged as more variable on smaller spatial scales in this study.

### *Regional differences in variance spectra*

Notwithstanding the spatial confounding of regional scale comparisons, species distributions in the lower topographical complexity region (southwestern England and Wales) had higher β values on average than in higher coastline complexity (western Scotland), in line with the hypothesis that scales of spatial variability in species abundance depend on the physical template of the habitat.

### *Scales of spatial patterns and ecological processes*

The challenge still facing ecologists considering spatial patterns is to match these to the spatial scales of the processes causing such patterns. This is a commonly identified goal of early reviews of spatial ecology (Wiens 1989, Levin 1992), and one partly achieved for some systems dominated by particular processes, such as the effects of physical structure on biomass and primary production in phytoplankton (Denman and Powell 1984). Intuitively, good matches between spatial variance spectra in environmental variables such as temperature (Vasseur and Yodzis 2004) or nutrients (Bell et al. 1993) and biological responses such as population abundance can suggest the primary candidates for potential causative factors. Where these matches are combined with strong correlations, the evidence begins to grow. Similarity between spatial scales of variation in kelp abundance and pelagic primary productivity on the North American west coast, for example (Broitman and Kinlan 2006), and a strong correlation between these two responses suggested coastal upwelling as a common cause for both phenomena.

Correlations can be scale dependent, such as those between predators and prey (Fairweather 1988, Horne and Schneider 1995), and the nature of these scale dependencies can help identify the ecological mechanisms underlying the links. Furthermore, explicit consideration of the spatial scale of such associations can clarify conclusions based on correlation evidence, such as the influence of top-down vs. bottom-up control in responses to climate (Richardson and Schoeman 2004).

These patterns may suggest characteristic "domains of scale" (Wiens 1989) for particular ecological processes. When considered with variation over temporal scales, Stommel diagrams (Haury et al. 1978) can effectively show the scales over which processes operate and convey the complex nature of causal mechanisms. We have not attempted to create such a synthesis for northeastern Atlantic intertidal communities, though the variance spectra calculated show the summed effect of these influences on each species. Even without such a synthesis, the form of the scale variance spectrum for each species can give a useful indication of the most important factors influencing population abundance over the spatial scales of the study. High β values for abundance indicate dominance by processes varying over large scales (100–1000 km) such as climate, variation in pelagic primary productivity, or nutrients, while low β values suggest a greater importance of medium- to small-scale (10–100 km) processes, such as restricted dispersal or locally varying wave fetch (Burrows et al. 2008). Conclusions as to the most important structuring processes may depend on the spatial scales of particular studies. Analyses of spatial variance on smaller scales (1 m to tens of kilometers; Underwood and Chapman 1996) tend to emphasize the importance of small-scale processes such as aggregation, while large-scale analyses highlight the importance of larger scale processes (tens to thousands of kilometers; Broitman et al. 2001, Nielsen and Navarrete 2004). The majority of studies in marine intertidal and shallow subtidal habitats apparently show greater variability on smaller spatial scales (meters; reviewed by Fraschetti et al. [2005]). Our study did not include scales below 10 km, the scale of separation between study sites, and would likely show this relatively large small-scale variability had we included sampling at the scales of 1 m to 1–10 km.

Matching scales of variation to processes may be possible with this approach by determining associations between predictor variable and response variables at different spatial scales. Analysis of the spatial variance of residuals combined with regression modeling may allow the separation of contributions of different predictors to variance at each spatial scale.

Ultimately, sets of ecological mechanisms generating particular variance spectra may be species (Levin 1992) and location specific. Our analysis has shown, however, that some generalities are evident when considering species characteristics. Effects of dispersal mode and trophic level may be small and variable compared to the effect of overall abundance of the species in the study area, but that such differences exist promises much for future progress.

### Acknowledgments

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## APPENDIX A

Ordination of sampling sites using multidimensional scaling (MDS) based on distances between sites by sea and measurement of coastline fractal dimension (*Ecological Archives* E090-080-A1).

## APPENDIX B

Recovering spectral exponents from simulated data using repeated hierarchical analysis of variance over a range of nested spatial scales (*Ecological Archives* E090-080-A2).

## APPENDIX C

Modes of reproduction in intertidal species used in the analysis of spatial scales of variation as described by β values (*Ecological Archives* E090-080-A3).

## SUPPLEMENT

The R code for simulating 2-D data with known spectral exponents, sampling, and ANOVA estimation of β (*Ecological Archives* E090-080-S1).